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THE RELATION OF THE EYES TO CHROMATOPHORAL ACTIVITIES.

By G. H. Parker, F. A. Brown, Jr., and J. M. Odiorne.
Biological Laboratories, Harvard University.

With One Plate.

(Continued from page 3 of cover.)

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1. Introduction.

In the course of three independent investigations on the color changes in animals we were impressed with the remarkable uniformity of response to loss of the eyes as shown by the several animals under consideration. When it is recalled how diverse the details of chromatophoral control have proved to be, not only between representatives of different groups of animals but between even closely related species, the great uniformity of the response to the loss of the eyes is truly surprising. The animals upon which we worked were the common frog, *Rana pipiens* Schreber, the shrimp, *Palaemonetes vulgaris* (Say), and two fishes, *Fundulus heteroclitus* (Linn.) and *Ameiurus nebulosus* (Lesueur). The details of the chromatophoral responses of these animals to the loss of the eyes will be discussed on the following pages.

The importance of the eyes in this type of reaction appears to have been pointed out first by Lister (1859, p. 638), who, in describing the results of his experiments on enucleated frogs, remarked that what he had seen "indicated pretty clearly that the eyes are the only channels through which the rays of light gain access to the nervous system so as to induce changes of colour in the skin." This conclusion was subsequently arrived at independently by Pouchet, who in a most important series of papers published between 1871 and 1880 demonstrated the necessity of the eyes in the color responses of fishes and crustaceans and further showed in the fishes, at least, that the whole reaction was dependent upon the sympathetic, or better the autonomic, nervous system. So complete and so full were Pouchet's proofs of the nervous control of chromatophores that for many years after his time no one suspected any other means to this end.

In 1898 Corona and Moroni showed that adrenalin when introduced into the blood of a frog had a profound effect upon its color cells. This unique observation was subsequently confirmed by Lieben (1906), who made a still further investigation of the subject. Comments by Fuchs (1914) on these two pieces of work led Redfield (1918) to study

the effects of adrenalin on the chromatophores of the lizard, Phrynosoma, with the result that this hormone was found to be a potent agent in inducing chromatophoral change.

Other such substances were likewise soon shown to be of great importance in color responses. Through the work of Adler (1914), Smith (1916), and Allen (1917) the technique of hypophysectomy on larval amphibians was developed, and it was pointed out that hypophysectomized individuals were always very light colored. The significance of this change from the standpoint of internal secretions and the chromatophore system was first indicated by Atwell in 1919. Two years later Swingle (1921) observed that tadpoles became dark when a part of the pituitary gland was transplanted into them. Hogben and his associates were thereby led to an extensive and thorough investigation of the pituitary gland and its secretions in relation to chromatophoral changes with results that were truly revolutionary. These, when coupled with the generally negative outcome of experimental nerve-cutting, led Hogben (1924, p. 92) to conclude that the color changes in amphibians involve little or no direct innervation and depend upon fluctuating amounts of pituitary secretion. In later studies that were carried on by Hogben and Slome (1931) on the South African clawed toad, Xenopus, a dual endocrinal control of amphibian color change was suggested, the pituitary and some second unknown factor, but even in this instance the added element was still regarded as humoral in character. Thus in amphibians, at least, the nervous interpretation of chromatophoral control was in large part abandoned for one based upon special hormones, or what are now called neurohumors.

At about the same time that the amphibian chromatophores were being shown to be under the control of neurohumors the same was being done for the color cells of crustaceans. In 1925 Koller made an interesting observation on the shrimp Crangon in that he noticed that an individual of ordinary coloration after having eaten another shrimp yellow in tint assumed a yellow color. This change suggested to him the possibility that the blood of the originally yellow individual contained a substance which on being transferred to that of the other shrimp induced it to become yellow. He was, therefore, led to experiment with the transfusion of blood and made the important discovery that when the blood from a dark shrimp was injected into the body of a light one the latter quickly became dark, though blood from a light shrimp had no effect whatever on the color conditions of another light one. He was, therefore, led to believe that the color changes in

crustaceans were influenced, and p rhaps controlled, by internal secretions and that consequently any final study of these changes called for a new type of attack with an appropriate technique. In 1928 Perkins made the important discovery that the eye-stalks of Palaemonetes contained a substance which when extracted in sea-water and injected into the blood of a dark individual would induce it to turn light. This discovery was further demonstrated in Crangon by Koller (1928), who declared that in this shrimp an organ for the production of an expanding hormone was to be found in the rostral region of the animal. These important results were confirmed with slight variations in detail by several subsequent workers, who were, further, unable to find any evidence whatever for the older view that the chromatophores of crustaceans were under the direct control of nerves. Thus the belief steadily gained ground that the crustacean chromatophoral system is organized on a purely neurohumoral basis.

Notwithstanding the validity of this conclusion and the recent extensive growth of evidence in favor of it as applied, for instance, to such animals as crustaceans and amphibians, it still remains true that in many fishes and lizards a nervous control of chromatophores can be most easily demonstrated. It is, therefore, held by a number of recent workers that chromatophores as a whole are subject to two sets of influences, nervous and humoral, and that in certain instances one set predominates and in others, the other one. A new approach on this problem, which seems to have been in the mind of Giersberg (1930), has been rather fully developed by one of us (Parker, 1932) under the name of neurohumoralism. According to this view, the first step in the color changes of actively chromatic animals is stimulation of the eye, from which nervous impulses pass either to glands of internal secretion whose products, the neurohumors, are then carried in the blood to the appropriate chromatophores or over nerves to these effectors which are excited by secretions, also neurohumors, from the terminals of these nerves, and not by what might be called direct nervous action. Thus all chromatophoral systems are in each instance partly nervous and partly humoral and differ chiefly in the extent to which each of the two elements enters into their organization.

The eyes and their relations to chromatophoral responses will be taken up in the present paper from this most recent standpoint. An attempt will be made to show the broad relations of the eyes to color changes, and this will be undertaken not simply from what we have found on the four animals named but also from what earlier workers have contributed. Three summaries of earlier investigations are

given in tabular form, one each for amphibians, for crustaceans, and for fishes. The tables are, of necessity, not complete though they represent a reasonably full survey of past work. Their omissions are chiefly due to our inability to decide with certainty what was the real meaning of some of the earlier workers. This is especially true of the column for "darkness," where it was often impossible to decide whether in a given reference it was intended to state that the eyeless animal had been exposed to complete absence of light or to a condition of only relative darkness. An attempt has been made to keep fairly close in the tabulation to the descriptive expressions of the various investigators, but here too the necessity for abbreviation may have led us to represent the original observation imperfectly. The term "dark" in the table stands for a similar expression in the original records and is regarded as essentially equivalent to the descriptive term "expanded" as applied to chromatophores. Notwithstanding the limitations necessitated by the tables, it is believed that they represent a general survey of the subject such as could be obtained in no other way.

2. In Amphibians.

The common spotted frog, *Rana pipiens*, shows, like other members of its genus, a well marked range of color changes. These changes affect, of course, the lighter parts of its skin not so much its permanent, large, dark spots. In an illuminated glass-vessel with white walls and water about a centimeter deep a normal spotted frog in a few hours acquires a relatively light tint and, with very slight fluctuations, re-

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Explanation of Figures.

All figures are from *Rana pipiens*. We are indebted to Dr. F. M. Carpenter for the photographs.

Figures 1, 2, and 3 are from the same frog in different states.

Figure 1. Normal frog in the light state.

Figure 2. Eyeless frog showing the partly dark state.

Figure 3. Normal frog in the dark state.

Figures 4, 5 and 6 are microscopic views of the melanophores in the web of a frog's hind foot.

Figure 4. Melanophores with fully concentrated pigment from a normal light frog. (Figure 1).

Figure 5. Melanophores with partly dispersed pigment from an eyeless frog. (Figure 2.)

Figure 6. Melanophores with fully dispersed pigment from a normal dark frog. (Figure 3.)

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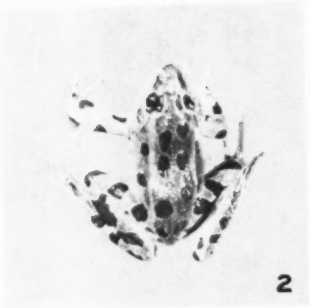
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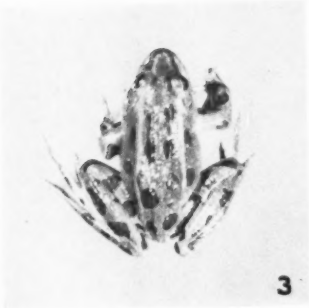
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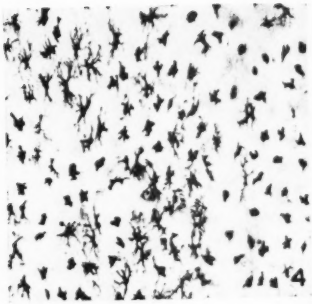
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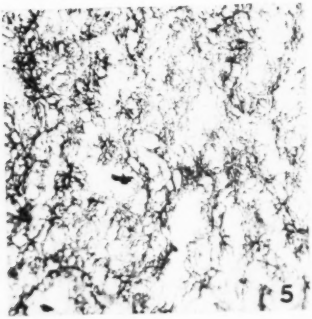
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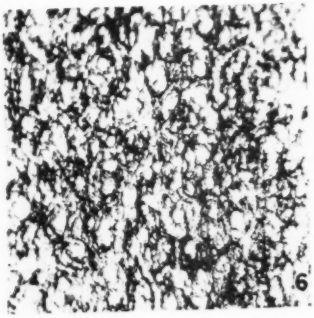
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mains persistently of this tone (Fig. 1). In a similar vessel but with black walls, the normal animal assumes a deep brownish tint (Fig. 3) and maintains this with little change indefinitely. The tests from which these records were taken, ran over nearly two weeks. They were carried out in a laboratory provided with artificial electric light that was operated day and night. The temperature was approximately 20° C.

Frogs that had been tested in this way were eventually enucleated, and in carrying out this operation it was found convenient first to stupefy the animals by keeping them for about a quarter of an hour in a mixture of ice and water. Under these circumstances they soon become very torpid and the operation of enucleation can be easily and satisfactorily performed. The frogs recover from the cold rapidly and, as no drug has been used, they quickly return to a normally active state. Within a few days after the operation their eyelids heal and such a frog, if fed from time to time, will live for many months.

After enucleation the animals, having been dark from the cold water, passed at once into a moderately dark phase without showing the initial light stage recorded by several workers (Lister, 1859; Kropp, 1927). The omission of this initial light condition is to be attributed to our method of stupefaction. The final tint of the animals (Fig. 2) was darker than that midway between the extremes of light (Fig. 1) and of dark (Fig. 3) but never reached the maximum depth of color. The transparent web of the foot in the enucleated individual showed a rich branching of the melanophores (Fig. 5), but not by any means so rich as that seen at maximum darkness (Fig. 6). It was very much more pronounced than the slight branching seen in light individuals (Fig. 4).

Enucleated frogs were tested in pairs to ascertain whether they showed color changes to any degree. Six pairs, the members of each pair having been closely matched in tint, were put in six white-walled glass-vessels illuminated by electric lights from above and provided with a shallow layer of water. They were compared from time to time during the day and for a period of over a week. One mate of one pair died before the expiration of the test but the other five pairs survived with satisfactory results. Though each pair was started with both members of the same tint, in a day or so the two showed observable differences. These differences appeared to be slight fluctuations, one side or the other, of the dark tint already described as somewhat less dark than the maximum. At no time did these animals show the extreme lightness or darkness possible to normal frogs. The extreme

fluctuations of the enucleated individuals fell far short of those of normal ones.

A similar set of tests was run with enucleated frogs kept for a number of days in dark-walled illuminated vessels and with essentially similar results to those just recorded. As an outcome of these tests it was quite clear to us that an enucleated frog could spontaneously change its color in either a light or a dark direction, though to only a very limited extent. In this respect we can confirm the observations of Kropp (1927), but we have seen nothing to corroborate the view of Carnot (1896) that blinded frogs respond in course of time more or less fully to environmental changes. So far as we could judge, an enucleated frog was just as likely to turn slightly dark as it was to turn slightly light in an illuminated white vessel or in a black one. For this reason, we are not inclined to think that the photic sensitiveness of the skin of this animal (Parker, 1903) has any influence on its chromatophoral changes.

Our observations on the frog agree fairly well with those of earlier workers on this animal, on tadpoles, on Xenopus, and on Diemyctilus as given in Table 1. In most of these records the animals are said to darken finally after the loss of the eyes and to be more or less fluctuating in tint. We have seen nothing to support Biedermann's contention (1892) that the eyeless frog is essentially the same in its color changes as is the normal individual. In our tests eyeless individuals always fell far short of the usual chromatophoral range of normal animals.

Eyeless frogs when placed in complete darkness exhibited no special change of tint. They were of an intermediate dark tone and maintained this condition, as has been reported by other investigators (see Table 1).

That eyeless frogs do not lose their capacity for color change in consequence of the loss of their eyes can easily be shown by the injections of appropriate hormones. If into the lymph spaces on the back of a frog that has been eyeless for some weeks, 0.2 cc. of adrenalin (Parke, Davis & Co.) is injected the animal becomes light tinted in from ten to fifteen minutes. The tint attained is in all respects like that seen in a normal frog after a corresponding injection. On injecting pituitary extract (Parke, Davis & Co., obstetrical preparation) into an eyeless frog it becomes dark to a maximum degree, which is a much deeper tint than that ever attained by such individuals under ordinary circumstances. Hence, we conclude that the eyeless condition has in no way disturbed the power of chromatophoral changes in the frog.

TABLE 1.

AMPHIBIANS.

States of the melanophores in various eyeless amphibians in light and in darkness, as recorded by various investigators. The forms are referred to under their common names or their generic names, and the references are arranged for the most part historically with dates agreeing with those in the bibliographies.

Investigator	Date	Amphibian	Eyeless	
			In Light	In Darkness
Lister	1859	Frog	Light then dingy	Darkish
Dutartre	1890	Frog	Changeable	
Biedermann	1892	Frog	Same as normal	
Carnot	1896	Frog	Follows environment	
Rogers	1906	Diemyctilus	Dark	Dark
Babák	1910	Frog tadpole	Very dark	
Babák	1910	Amblystoma larva	Dark	Light
Babák	1913	Amblystoma larva	Dark	Light
Laurens	1914	Amblystoma larva	Dark	Light
Laurens	1915	Amblystoma larva	Dark	Light
Laurens	1917	Amblystoma larva	Dark	Light
Hooker	1914	Frog tadpole		Contracted then expanded
Hogben, Winton	1923	Frog		Mostly dark
Hogben	1924	Frog	Dark	
Kropp	1927	Frog	Light, then follows environment	
Kropp	1927	Frog tadpole	Dark	
Slome, Hogben	1928	Xenopus	Dark	Intermediate
Hogben, Slome	1931	Xenopus	Dark	

The only eyeless amphibian whose chromatophoral responses fail to agree in general with those already discussed is the larval Amblystoma. This animal has been studied by both Babák (1910) and Laurens (1915, 1917). The eyeless larvae of this form are stated by both these workers to become dark in ordinary illumination. In this respect they agree with other amphibians, as Table 1 shows, but instead of remaining dark when placed in darkness, as most amphibians do, they become light. This response to darkness is very striking and has a bearing on the question we are discussing, because it shows that beside the eye some other factor is concerned with chromatophoral control in the young Amblystoma. Such, indeed, may be true

to some degree of other amphibians (see Frog tadpole according to Hooker, 1914, and Xenopus according to Slome and Hogben, 1928, in Table 1). But however this may be, the supremacy of the eye in the group as a whole cannot be denied. All blinded amphibians in ordinary daylight assume a fairly dark to a full dark tone and exhibit under these conditions only minor fluctuations. The older workers have at times discussed this situation on the assumption of an interference with a direct nervous control, but in our opinion it results from an interruption in the secretory mechanism that has to do with the formation of the necessary neurohumors, for, notwithstanding the recent contention of Karásek (1933) that nerves play a direct part in the chromatophoral system of amphibians, we regard this control as secretory and only secondarily concerned with nerves.

3. In Crustaceans.

The all-importance of the eyes in the control of the chromatophores of crustaceans was first demonstrated in Palaemon by Pouchet in 1872. Pouchet's studies on the color changes of fishes had shown him that the autonomic nerves were the means of communication between the eyes and the chromatophores and he was, therefore, led to believe that impulses originating in the eyes of shrimps must reach and control the distant chromatophores also by means of nerves. This opinion he held notwithstanding the fact that all his experiments on the cutting of nerves in crustaceans yielded only negative results (1872 to 1876). The majority of investigators of the chromatophoral system in crustaceans who followed Pouchet, accepted his view though they too failed to find any supporting evidence from the standpoint of nerve cutting (Mayer, 1879; Matzdorff, 1883; Fröhlich, 1910; Menke, 1911; Degner, 1912). It was not till 1925, as already stated, that Koller began to suspect a humoral control of crustacean chromatophores. In 1928 Perkins subjected Palaemonetes to an exhaustive series of tests in nerve cutting and with entirely negative results. In consequence both he and Koller finally were led to declare against a nervous interpretation of these activities and in favor of a purely humoral one. Our view coincides with theirs. So far as the crustaceans are concerned, their chromatophoral system appears to be entirely free from direct nerve intervention and is organized on a neurohumoral basis.

Palaemonetes vulgaris, the shrimp studied by us, possesses the usual type of crustacean chromatophore, namely, one composed of a number of conjoined cells containing several pigments. The pigments

in *Palaemonetes vulgaris* are of four kinds: red, yellow, blue, and white. In action these four can be shown to be fully independent one of the other and hence require four independent exciting mechanisms. By means of these color-changes, singly or in combination, Palaemonetes may adapt itself well to backgrounds of white, yellow, red, blue, green, dark gray, or black. These responses involve not only a migration of pigment but also a production and a destruction of this material.

A neurohumor producing a concentration of the white pigment in Palaemonetes occurs in its eye-stalks and in some tissue in the anterior region of the cephalothorax. Neurohumors for the concentration of the red and the yellow pigments come from certain central nervous organs. The source of the neurohumor for the concentration of the blue pigment has not been discovered. Palaemonetes, unlike Crangon (Koller, 1928), appears to produce no neurohumors for the dispersion of its pigments. This process is believed to follow from the absence of the appropriate concentrating neurohumor and to be a property of the chromatophore itself.

In Crangon where, according to Koller, there is a dispersing as well as a concentrating neurohumor the condition is more nearly parallel with that in the frog, in which, in addition to a pronounced dispersing neurohumor, there is reason to believe that a concentrating one may occur (Slome and Hogben, 1928).

Palaemonetes, with its four sets of mutually independent pigments, presents a much more complex picture than that of the frog, with only melanophores. This complexity is to be seen in the responses following the removal of the eyes. As would be expected, the loss of one eyestalk shows little or no effect on the color changes, but when both are removed the shrimp assumes a dark reddish brown tone, which is ordinarily persistent. This state is brought on by a gradual and finally complete dispersion of the yellow and red pigments and by a formation of blue. The white pigment shows no special response. The resultant dark coloration was found to maintain itself with no apparent change when the animal was kept in an illuminated black-walled vessel, a similar white-walled vessel, or in complete darkness.

The dark condition of the eyeless Palaemonetes is in agreement with what has been recorded for most other crustaceans under like circumstances (see Table 2). The exceptions to this statement, as can be seen by inspecting the table, are Idotea, whose chromatophoral system is apparently not very active, and the very remarkable species *Hippolyte varians* studied by Keeble and Gamble (1900, 1904) and by

TABLE 2.

CRUSTACEANS.

States of the chromatophores in various eyeless crustaceans in light and in darkness as recorded by various investigators. The forms are referred to under their generic names, and the references are arranged for the most part historically with dates agreeing with those in the bibliography.

Investigator	Date	Crustacean	Eyeless	
			In Light	In Darkness
Pouchet	1872	Palaemon	Fully dark	
Pouchet	1872	Palaemon	Fully dark	
Pouchet	1874	Palaemon	Red	
Pouchet	1876	Palaemon	Dark red	
Jourdain	1878	Nika	Dark red	Red
Mayer	1879	Idotea	Unchanged	
Keeble and Gamble	1900	Hippolyte	Contracted	Nocturne
and	1900	Palaemon	Expanded	Contracted
Gamble and Keeble	1904	Macromysis	Expanded	Contracted
Przibram	1902	Carcinus	Red	
Bauer	1905	Idotea	Intermediate	Midgray
Fröhlich	1906	Palaemon	Dark brown	Red brown
Fröhlich	1910	Palaemon	Dark brown	Red brown
Megušar	1908	Gelasimus	Dark	
Megušar	1912	Palaemonetes	Red brown	
Megušar	1912	Palaemon	Dark	
Megušar	1912	Potamobius	Dark	
Minkiewicz	1908	Hippolyte	Contracted	
Doflein	1910	Leander	Brown	Reddish
Tait	1910	Ligia	Fully dark	
Degner	1912	Crangon		Expanded
Bauer and Degner	1913	Leander	Brown red	Expanded
Piéron	1913	Idotea	Expanded	
Piéron	1914	Idotea	Expanded	
Koller	1928	Crangon	Intermediate	
Koller	1930	Crangon	Intermediate	
Perkins	1928	Palaemonetes	Dark	Expanded
Smith	1930	Macrobrachium	Expanded	
Brown	1933	Palaemonetes	Dark	Dark

Minkiewicz (1908). This remarkable shrimp stands out in contrast with other crustaceans in the great variety of its color phases and patterns, its marked daily rhythm which persists some time after the natural light and darkness relations have been interrupted, and in its assumption of a uniform, nocturnal, blue phase in darkness irrespective of its previous diurnal state. With the loss of its eye-stalks it passes over into a permanent "nocturne," that is, a state in which

its chief chromatophores are contracted. This state is in strong contrast with, for instance, that of Palaemon and Macromysis, as well as with other species of Hippolyte, all studied by Keeble and Gamble and in which the loss of the eye-stalks is followed by darkening. *Hippolyte varians* must, therefore, be set aside as a species whose chromatophoral organization is in a measure unique and in that sense not easily compared with other crustaceans.

Excepting this remarkable form, whose chromatophoral activities are still worthy of further study, all the other crustaceans with active chromatophoral systems and recorded in Table 2, agree in becoming more or less completely dark on the loss of the eye-stalks. This operation, like the corresponding one in the frog, seems to bring to an almost full standstill those processes that modify neurohumoral activity in relation to environmental color adaptation. The operation not only checks these processes but, as has been pointed out by Koller (1930), it removes from the animal what seems to be the most important source of the neurohumors, the eye-stalk itself. Yet, notwithstanding this profound change, most crustaceans respond to the loss of the eye-stalks with a darkening of the body as remarkable as it is uniform.

4. In Fishes.

If the chromatophoral systems in amphibians and in crustaceans yield very strong evidence of what is usually regarded as an almost strictly humoral system, the fishes exhibit conditions that are equally favorable for nervous control. The turbot was the first form which in the hands of Pouchet (1871) yielded evidence of a most convincing kind that its dermal melanophores were controlled by nerves. When cuts were made across bundles of nerves in this fish, the pigment in the melanophores in the denervated region became dispersed and thus was produced a dark area corresponding to that of denervation. This experiment was tried by Pouchet on a variety of fishes and with results confirmatory of his first observations. It has been repeated by a large number of later workers on many fishes and with great uniformity of outcome.

Nevertheless, Meyer in 1931 pointed out the remarkable fact that if the serum of a flatfish that had been darkened by having been kept one or two weeks in an illuminated dark-walled aquarium was injected into a light-tinted fish, within five minutes a dark spot appeared in the region of injection. This spot continued to increase in intensity for half an hour or so, after which it slowly disappeared. In a similar

way, serum from a light-tinted fish when injected into a dark fish was said to produce a temporary light spot. This is strong evidence in favor of a humoral interpretation of color changes, and from a group of fishes which of all others seemed to be the most favorable for the nervous plan of color control. The clue contained in these observations was followed up by several investigators, and it soon became evident that fishes were by no means uniform in the methods by which their chromatophores were controlled. In certain instances they exhibited good examples of what had been regarded as direct nerve effects and in others conditions were found where humoral agents seemed to play at least some part. Thus in Mustelus, the dark phase of this fish was shown to be called forth by a pituitary neurohumor (Lundstrom and Bard, 1932) whereas the light phase was due to direct nerve action (Parker and Porter, 1934). In Ameiurus the dark state was due in part to direct nerve action and in part to a pituitary hormone and the light phase to direct nerve action only (Parker, 1934). In Fundulus, Matthews (1933) showed that the serum from an individual of one extreme tint has no effect upon another of the opposite tint, and yet Parker (1934) has given good reason for the opinion that the color changes in this fish are induced by neurohumors that come directly from the nerves. With this diversity of control in mind, our own observations on the relations of the eyes to color changes in Fundulus and in Ameiurus will now be considered.

Normal *Fundulus heteroclitus* has a well defined dark phase as well as a light one corresponding to the dark or the light character of its environment. When both eyes are removed Fundulus changes irrespective of its previous state to a dark tint that is not quite so dark as the maximum shade of this fish. This tint is maintained unchanged in illuminated vessels with black walls as well as in those with white walls. Our results confirm those of Wyman (1924) and of Sumner (1933) but not those of Parker and Lanchner (1922), according to whom blinded fishes were found to be light. This difference is to be attributed to a difference in the technique used by Parker and Lanchner, as contrasted with other workers. Whereas most workers blinded their fishes by cutting the optic nerves or by enucleation, Parker and Lanchner attempted this by covering the fish's eyes with an impervious paste. This technique was, without doubt, inadequate and in consequence of the accidental leakage of light into the eyes rendered the fish light.

Eyeless Fundulus maintain their dark tint under all circumstances

excepting when they are in darkness. If a number of Fundulus whose optic nerves have been cut are transferred to a dark room they soon become slightly but noticeably light. This new condition is retained as long as they are kept in the dark but is lost by a return of the fishes into the light. This rather remarkable condition resembles that recorded for Amblystoma larvae by Babák (1910) and by Laurens (1914, 1915) where blinded individuals, though dark in the light, become light tinted in darkness. None of these changes in Fundulus are concerned with any obvious production or destruction of melanin such as is known to occur in this fish (Odiorne, 1933) and in Lebistes (Sumner and Wells, 1933) in the course of time. They belong to what are ordinarily called physiological, rather than morphological, changes.

Ameiurus, like Fundulus, exhibits two well marked extremes of color, dead black on the one hand and a light greenish yellow on the other. It changes in response to environmental differences as does Fundulus, but the rate of change is much slower in Ameiurus than in Fundulus. When catfishes are enucleated they assume a very dark tint, though not the maximum shade, and they retain this condition in any illuminated aquarium irrespective of background (Van Heusen, 1917; Bray, 1918; Pearson, 1930). Like Fundulus, they become slightly lighter when they are put in complete darkness and gain in depth of color when they are returned to the light. Ameiurus, like Fundulus, can increase or decrease to no inconsiderable amount its store of melanin, but the changes thus far described for this fish are due primarily to the shifting of melanin within its chromatophores and not to a change in the amount of this pigment.

Both Fundulus and Ameiurus respond to the loss of eyes by assuming a relatively constant and moderately dark tint. In this respect they agree with the great majority of fishes whose conditions are given in Table 3.

An inspection of Table 3 will show that very few fishes are exceptions to the rule that enucleation is followed by an early darkening of the skin. Pouchet (1877, 1878, 1880) discovered the remarkable fact that in the trout the removal of one eye, which in most fishes has no observable effect on the color changes of the animal, resulted in a contralateral darkening in this form, a condition in part associated with the optic chiasma. Pouchet's discovery was confirmed by von Frisch (1911), who attributed to abnormal conditions the inability of Steinach (1891) to find similar results. The slowness to respond on the part of certain flatfishes is probably accountable for some records in which these forms were not reported as darkened by blinding

TABLE 3.

FISHES.

States of the melanophores in various eyeless fishes in light and in darkness as recorded by various investigators. The forms are referred to either under their common names or their generic names and the references are arranged for the most part historically with dates agreeing with those in the bibliography.

Investigator	Date	Fish	Eyeless	
			In Light	In Darkness
Pouchet	1871	Turbot	Reddish	
Pouchet	1872	Turbot	Reddish	
Pouchet	1874	Sole	Dark	
Pouchet	1874	Carassius	Dark	
Pouchet	1874	Aspius	Dark	
Pouchet	1874	Gobio	Dark	
Pouchet	1876	Turbot	Red	
Pouchet	1877	Trout	Contralateral dark	
Pouchet	1880	Trout	Contralateral dark	
Lode	1890	Trout	Dark	
Steinach	1891	Pleuronectes	No darkening	
Steinach	1891	Trout	Variable	
Mayerhofer	1909	Esox	Deep green	Lightens
Šecerov	1909	Nemachilus	Dark	
Franz	1910	Pleuronectes	Very dark	
Bauer	1910	Flatfish	Intermediate	Intermediate
Buytendijk	1911	Turbot	Dark or Light	
Sumner	1911	Rhomboidichthys	Dark	
Sumner	1911	Lophopsetta	Dark	
von Frisch	1911	Phoxinus	Dark	Lightens
von Frisch	1911	Carassius	Dark	
von Frisch	1911	Salmo	Contralateral dark	Dark
von Frisch	1911	Perca	Dark	
Polimanti	1912	Rhombus	Variable	
Van Heusen	1917	Ameiurus	Dark	
Bray	1918	Ameiurus	Dark	
Murisier	1920	Salmo	Dark	
Parker & Lanchner	1922	Fundulus	Light	Light
Wyman	1924	Fundulus	Dark	
Tozawa	1924	Goldfish	Dark	
Abolin	1925	Phoxinus	Moderate expansion	
Pearson	1930	Ameiurus	Dark	
Sumner	1933	Fundulus	Dark	
Parker and Porter	1934	Mustelus	Dark	

(Steinach, 1891; Bauer, 1910; Buytendijk, 1911; Polimanti, 1912). What appears to be a real exception among fishes to the rule that enucleation is followed by darkening is seen in Phoxinus. On the

loss of its eye this fish is stated by von Frisch (1911) to be first dark and then variable. Abolin (1925) declared that after the loss of its eyes Phoxinus exhibited moderately expanded chromatophores. When it is recalled that after blinding the chromatophores of this fish will still respond with more or less appropriateness to environmental changes of color, its exceptional position must be evident. Its powers of chromatophoral response under such conditions has led to tests with the view of locating some photoreceptors other than the eyes to explain this state, a search that has pointed to the pineal organ, rather than the skin (von Frisch, 1911; Scharrer, 1928), as the part concerned. Thus Phoxinus is peculiar in several respects and from this standpoint is perhaps best set off against other fishes, the loss of whose eyes seems always to be associated with a moderate or full darkening of the skin. As with amphibians and crustaceans, the loss of the eyes in most fishes brings to a standstill the mechanism of chromatophoral change and the whole system rests in a state of partial or complete dispersion of pigment.

5. Discussion.

A survey of the chromatophoral responses of the four animals upon which we worked is shown in Table 4. Here it will be seen that so long as the eyes were intact these animals responded to a white or a black illuminated background by appropriate changes and with great uniformity. In the white-walled vessel all were light-colored; in the black-walled one all were dark. In total darkness the uniformity of these animals disappeared. After the loss of the eyes the distinction in response to illuminated white or black surroundings was entirely

TABLE 4.

Chromatophoral Responses of Four Animals.

Rana, Palaemonetes, Fundulus, and Ameiurus, with or without eyes, kept (1) in an illuminated black-walled vessel, (2) in an illuminated white-walled vessel, and (3) in total darkness.

Animal	Rana	Palaemonetes	Fundulus	Ameiurus
Condition—With Eyes				
White-wall Vessel	Light	Light	Light	Light
Black-wall Vessel	Dark	Dark	Dark	Dark
Darkness	Mid-dark	Variable	Light	Lightish
Condition—Without Eyes				
White-wall Vessel	Mid-dark	Dark	Mid-dark	Mid-dark
Black-wall Vessel	Mid-dark	Dark	Mid-dark	Mid-dark
Darkness	Mid-dark	Dark	Light	Lightish

obliterated and each form responded the same to the two kinds of environment. The condition in darkness was again diverse. It is clear from these results that the loss of the eyes brings about an almost complete cessation of the characteristic chromatophoral activities. Apparently the eyes are the chief means of initiating these responses, as was long ago maintained by Lister (1859). But they are not the only means to this end, for both eyeless Fundulus and Ameiurus lighten when placed in darkness, though they do not respond characteristically to different illuminated environments. As was already pointed out, this condition is very pronounced in Phoxinus; but what the additional receptor is in this fish and the two studied by us, brain, pineal organ, or skin, has not as yet been finally determined.

The main result, however, is not to be seen in the exceptional peculiarities of the four animals under review, but in their uniform darkening after the loss of the eyes and when in the light. This type of response, which is also characteristic of almost all the animals recorded in Tables 1, 2, and 3, is a most remarkable condition, when one keeps in mind the great diversity of means whereby chromatophoral changes are induced. It suggests at once an underlying uniformity that in the understanding of these changes must be of more significance than the mere machinery of accomplishment.

To our minds, this uniformity lies in the chromatophore itself rather than in the exciting means, neurohumoral or otherwise. Spaeth (1916) some time ago advanced the proposition that melanophores are disguised smooth-muscle cells, a view that emphasized the many striking resemblances between these two types of effectors. But we believe that, notwithstanding these resemblances, chromatophores, including melanophores, have as much individuality as a type of effector as do other like elements, such as gland cells, ciliated cells, and so forth. If any comparison between chromatophores and other types of cells is to be made, it is more justly in the direction of amoeboid cells than in that of smooth-muscle cells. These cells, and even the amoeba itself, have most obvious resemblances to chromatophores. Any one who has watched the movements of particles in the endoplasm of a pseudopod of the amoeba cannot help but have been impressed with the resemblance of this type of movement to that of pigment granules in the process of a melanophore.[1]

[1] In this comparison it is not meant to imply that the dispersion and concentration of pigment in a chromatophore is like the extension and withdrawal of pseudopods in the amoeba. The point of resemblance between the two types of cells is in the peculiar movement of the particles within their processes, be these processes temporary or permanent.

This comparison with the amoeba is, we believe, more than a mere superficial resemblance. The views on chromatophoral activation advanced in this paper, together with the general survey of the subject, have led us to conclude that when a chromatophore is released from external control, as for instance by enucleation, it gravitates more or less of itself to a fairly fixed state. This state is one with fully or almost fully dispersed pigment. We do not regard this state as a resting one, for we do not favor the view that there really is such a state in chromatophores. The dispersed chromatophoral state is, in our opinion, comparable to the condition of an amoeba with extended pseudopods. As is well known, when such an animal is vigorously stimulated it responds by the retraction of its pseudopods and becomes approximately spherical in form. This corresponds in our comparison to the condition of a chromatophore with concentrated pigment and might be regarded as representing a state of full activity as contrasted with that of full rest. But, as already stated, we are not inclined to regard any state of the chromatophore as one of rest or activity such, for instance, as can be declared for striped muscle. We regard chromatophores as cells or cell-aggregates which may be excited by external means (neurohumors) to concentrate or to disperse their pigment. When they are freed from external influences they of themselves gravitate, so to speak, to a condition of fully or almost fully dispersed pigment.

If this view of chromatophoral activity is correct two sets of agents must be concerned, on the one hand concentrating and dispersing neurohumors and on the other the innate dispersing action of the chromatophore itself. It follows from this view that the process of pigment dispersion would depend upon two factors one external, a neurohumor, and the other internal, the dispersing activity of the chromatophore, while pigment concentration would be excited by only a single external factor, a neurohumor. It is remarkable that in the few instances where the processes of pigmentary concentration and of dispersion have been timed, dispersion, the process assumed to be under double control, is more rapid than concentration, that assumed to be under a single agent.[2] These observations on the times

[2] The time necessary for pigment concentration and pigment dispersion in chromatophores has been determined for Anolis by Carlton (1903), for Phryn-

involved in change, still further disposed us to look with favor on the scheme of pigment concentration and dispersion suggested by us in this paper. They do not, however, lead us to designate any condition of the chromatophore as especially one of rest or of activity, as may be done with cross-striped muscle. Such distinctions are in our opinion inappropriate for chromatophores.

Summary.

1. Eyeless specimens of *Rana pipiens*, of *Palaemonetes vulgaris*, of *Fundulus heteroclitus*, and of *Ameiurus nebulosus* quickly attain a dark coloration and in the light retain this tint irrespective of the environment.

2. This dark condition is true of the majority of other eyeless amphibians, crustaceans, and fishes under like conditions.

3. In darkness eyeless Rana and Palaemonetes are of the same tint as in the light, but Fundulus and Ameiurus assume a lighter shade, showing that there must be some other element than the eye that influences their chromatophores.

4. The concentration of pigment in chromatophores is believed to be due to one factor, a concentrating neurohumor; its dispersion to two, a dispersing neurohumor and the innate action of the chromatophore itself.

5. Chromatophores, unlike striped muscle, exhibit no state that may be rightly called a state of rest, as opposed to one of activity.

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osoma by Parker (1906), for Fundulus by Parker (1934), and for Mustelus by Parker and Porter (1934) as follows:

	Concentration	Dispersion
Anolis	25 min.	4 min.
Phrynosoma	30 min.	15 min.
Fundulus	4.6 hrs.	1.8 hrs.
Mustelus	48 hrs.	2 hrs.

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